

Studies of Malesian Pandanaceae, I

Polymorphism in *Pandanus odoratissimus* L.f. of Asia

by

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In Ridley's Flora of the Malay Peninsula, vol. 5, (1925) the common pandan of beaches and coasts of Malaya is described under the name of *Pandanus fascicularis* Lamarck, and placed in the section Keura. That section, since it includes the type species of the genus, must now be called section *Pandanus*, and *P. fascicularis* is considered a synonym of *P. odoratissimus* L.f., which is the type species of the genus. *P. odoratissimus* has had a history of considerable confusion. It has an acknowledged list of many synonyms, but it has also been frequently misapplied to quite different species. It has at one time or another been considered as equivalent to *P. tectorius*, with now one and now the other name considered as a synonym. It has been used as a kind of receptacle for undeterminable collections and for sterile cultivars. The result of this historical confusion has been the obscuring of the real specific characters and the true distribution of the species.

Recently a considerable number of species have been described from Malaya and adjacent or nearby areas in South-east Asia by Dr. H. St. John in *Pacific Science* (1959-65). In attempting to write up the Malayan Pandanaceae, it of course became necessary to undertake a study of these species. To do so, not only have the holotype specimens in the Herbarium of the Botanic Gardens, Singapore, been examined, but travel to some of the type localities was made to study the living plants. Some types were seen at the Arnold Arboretum. In some cases I have not seen the types, but the descriptions are so full, and the illustrations so good, that little doubt as to the character of the plant was left.

The conclusion I have reached is that only one species of section *Pandanus* is wild in Malaya, but that it is represented by several forms, most of which are so minor in distinctiveness, and so clearly united by transitional forms, that it is impossible to regard them as separate species. Since this view appears to be so greatly at odds with the treatment in *Pacific Science*, it has seemed necessary, as well as valuable, to discuss the situation at length, and especially to set forth all the reasons available for the reduction of so many species to *Pandanus odoratissimus* L.f. Taxonomists often list new synonyms with a remark or two such as "indistinguishable" or "differing only in the somewhat larger

leaves", and not rarely give no remark at all, assuming evidently that none is required. On the contrary, it seems to me that listing a name as a new synonym requires explanation. Therefore I present in this paper the data which have convinced me of the need to bring the indicated species to synonymy.

Important Taxonomic Characters. The characters which are used in the discrimination of species in the whole genus are not all of use in the present case. For example, the highly important characters of *leaf-tip shape* and of *armament of ventral pleats* are of no value among the forms considered here, since they are identical (all leaves have long, narrowly attenuate, flagellate tips, and unarmed ventral pleats). The habit and habitat characters differ slightly, but far less than in other sections of the genus. The presence of a racemose or spicate female inflorescence likewise is of great importance, but in all our forms the cephalium is solitary on the peduncle. The fruits are syncarpous, with phalanges of several fused carpels, and none of the forms considered here has simple drupes. The stigmatic structure is of the same type throughout in our forms, as is evidenced by their inclusion in section *Pandanus*.

The remaining characters, which have been considered important in the original diagnoses of the species and in my own experience are as follows: (1) shape and dimensions of the cephalium; (2) length of the peduncle; (3) number and range, and median number (major carpel number) of carpels per phalange; (4) dimensions of phalanges; (5) presence or absence of fleshy mesocarp shoulders around middle of phalange; (6) color of phalanges; (7) presence or absence of lateral sutures in phalanges; (8) depth of apical sinuses between carpel apices; (9) position of endocarp within the phalange; (10) dimensions of the leaves; (11) number of veins in leaf (as counted near leaf midpoint); (12) color, size, and spacing of leaf prickles; (13) direction of midrib prickles.

The following remarks on the above characters precede a comparison of them in the species concerned.

1. Shape and dimensions of the cephalium. It should be superfluous to note that measurements of the character are useful only if full-grown cephalia are available. In addition it must be noted that (a) fruit-size decreases somewhat as the plants grow older; very old trees often produce cephalia as much as 40 per cent smaller than young, vigorous plants. Furthermore, adverse environmental conditions produce a size reduction; (b) the distinction between globose, subglobose, and ellipsoid cephalia is a very lax one; smaller cephalia are often concomitantly more globose.

2. Length of peduncle. This character appears to vary in much the same manner as cephalium size.

3. Carpel number. This is an important character, which I have discussed in another paper (1967). Briefly, it has been found that by plotting data from one cephalium in graphic form, the

carpels-per-phalange number on the horizontal axis and the number of phalanges on the vertical axis, a curve is obtained which typically begins at a relatively small carpel number, quickly rises to a peak, then more gradually descends to a relatively large number (Figure 5). Thus, of a cephalium bearing sixty phalanges, it may be found that three phalanges were composed of four carpels; 23 phalanges were composed of five carpels; 20 phalanges of six carpels; 8 phalanges of seven carpels; and 6 phalanges of eight carpels each. In this case, the "range" of carpel number would be 4–8, and the "major carpel number" would be 5. Ostensibly, cephalia showing different major carpel numbers are different in a taxonomic sense; but, as pointed out in the paper already referred to, the taxonomic function of this difference is often overestimated.

4. Dimensions of the phalanges. As pointed out above in sect. 1, size is partly a function of age and of environmental conditions, as well as of hereditary causes. Especially important is the dictum that all measurements be taken on ripe, full-grown material. For the sake of comparability, phalanges from the same part of the cephalium should be utilized; basal (peduncular region) phalanges are invariably shorter than average, as well as being curved, and have a greater than normal number of carpels.

5. Shoulders. The pulpy, firm expansion of the midregion of the phalange is conveniently termed shoulders. These are often eaten by insects on fruits still on the tree, and rather quickly "disappear" on dried or weathered phalanges. In my experience, the presence of shoulders on phalanges is a major character of *Pandanus odoratissimus*, and is correlated with other major characters such as the white color of the leaf prickles, the twin glaucous strips on the underside of the leaves, etc. Shoulders are either absent, or of a different shape and color, or are not correlated with other characters, in similar but distinct species.

6. Phalange color. Clearly, a good color terminology is required here; also it is important that fruits be fully ripe. In our species, the entire phalange becomes some shade of red-orange; but the last part to turn this color is the summit (carpel apices) of the phalange. The shoulders are often a deeper red than the rest of the phalange; and the extreme base may be yellowish.

7. Lateral sutures. By this is meant deep divisions between the carpels, visible in side view. Generally such sutures are absent in our species, though an occasional one or two occur. Phalanges with marked, deep, and regular sutures between carpels could indicate a different species.

8. Depth of apical sinuses between carpel apices. This character is a fairly important one, as it contributes largely to the overall impression one obtains when seeing a cephalium, or even loose phalanges, for the first time. Furthermore, it often is of specific importance. However, unless the depths concerned differ by more than just a few millimeters, they do not seem to merit overmuch

attention at the species level of distinctiveness. It must be pointed out that phalanges from the peduncular end of the cephalium will generally have shallower sinuses than phalanges from the mid-region or apex of the same cephalium.

9. Endocarp position. This too can be a significant character, as for example in discriminating such species as *Pandanus dubius* and *P. compressus*, or in the circumscription of *P. basilocularis*. Nevertheless, different positions may be attained in different ways; in some cases, extra growth of the apex of the phalange; in other cases, extra growth of the basal fibers; and both of these types of cases may be found to occur on one and the same plant at different times. More important for our discussion is the fact that since growth of the phalange continues at the base until the full length of the phalange is attained, an immature phalange will generally have an apparently sub-basal endocarp.

10. Leaf dimensions. These vary from several causes. Pandans have several categories of leaves: (a) prophylls and preliminary foliar bracts; (b) normal foliage leaves; (c) transitional leaves merging with inflorescence bracts; (d) seedling leaves; (e) juvenile leaves. It is generally useless to compare an organ of type (a) from specimen 1 with an organ of any other type from plant 2. Obviously, comparable structures must be compared. Besides this, older plants produce smaller leaves than younger plants. In general it may be stated that normal foliage leaves of unbranched juveniles may be up to four or five times as long, and half again to three times as wide, as leaves of adult plants.

11. Number of main longitudinal veins per leaf. The same cautions mentioned in sect. 10 should be heeded. Naturally, smaller leaves will have fewer longitudinal veins, even on the same individual.

12. Prickles. The underlying features of the prickles of the species under consideration is their white or very pale color. This character at once distinguishes these plants in the field. It is in marked distinction to the dark or merely pale green prickles of many other species, including the ones of the Eastern Pacific often lumped under the name *P. tectorius*. These white prickles are also relatively long, i.e. on the leaf bases of mature leaves they may exceed 6–7 mm. in length. Their spacing may be expressed as a range of distances between successive prickles at given positions (e.g., marginal prickles near leaf-base 6–12 mm. apart); or in terms of how many occur per unit (e.g., marginal prickles near base 3–4 per 10 cm.).

13. Direction of midrib prickles. In our species, the midrib prickles of the basal portion of the leaf are always retrorsely curved. This quickly distinguishes these plants from some related species and from some unrelated species (as well as from Cyperaceae).

Before proceeding with a comparative analysis of species, it is necessary to fix the character of *Pandanus odoratissimus*. This is no easy matter, since the description is very brief, and worst of all, it is based on the male plant. The type locality is Ceylon, so it may be expected that a collection made there of both male and female plants would establish the identity of the species. The fruit is needed, because nearly all subsequent descriptions emphasise the fruits. Luckily this has been done by Dr. St. John and we are therefore in a position to make the comparisons needed with Ceylon material.

Comparative analysis

The essential characters are set out in Table 1. In summary, it may be stated:

(1) Size range for cephalia is from 8.8 x 8.8 cm. in *P. globosus* and 9 x 8.5 cm. in *P. rubricoloratus* to 23 x 20 cm. in *P. hueensis*. Average size appears then to be about 16.8 x 14 cm. The only gap seems to be for *P. hueensis* and *P. vietnamensis*.

(2) Peduncular length varies from 9 to 40 cm., with the average length near 25 cm.

(3) Carpel number. Since the original data is not expressed in the form outlined earlier, only ranges can be given. These rarely cover more than 5 carpels difference between minimum and maximum in any one cephalium. The smallest number given is 4 (in 2 species); the largest number is 14 (in 2 species). The general range is thus 4–14, with 5–12 being far more common. A gap seems to exist between species with the "major carpel number" at 5, 6, or 7, and those at 9 or 11, but this seems uncorrelated with any other significant feature.

(4) Phalange size varies more or less continuously between 3.5 and 7 cm. long and 1.6 and 4.6 cm. wide. Phalange color is always some shade of red or red-orange, if fully ripe; if too young, yellow or green.

(5) Number of phalanges per cephalium ranges from 26 to 143, with figures between 60 and 90 apparently most common.

(6) None of these forms have regular, deep lateral sutures; most have none; a few have occasional shallow sutures.

(7) All forms have fleshy shoulders except those which are clearly immature. It is believed that these too would exhibit shoulders at full ripeness.

(8) Leaves range in length from 0.8 to 2.4 (or 3?) meters, and in width from 2.8 to 6.3 cm. All have pale or white prickles; many have dark or brownish tips on the prickles. The number of longitudinal veins in each half varies from 21 to 45 (in the known examples).

(9) Ecology. All forms are beach, coastal, or swamp species, near the sea. Geographically, they range from the Indian Ocean through S.E. Asia to Malesia.

In conclusion, it appears from this analysis that 9 species described from Malaya, one from Anamba Is., 10 from Vietnam, one from Hongkong, and four from the Maldive Is., can all be considered synonymous. Several are considered to be at least temporarily recognizable as forms. There follows a list of the synonyms and discussion of the forms and species maintained.

Description of Pandanus odoratissimus.

Pandanus odoratissimus Linnaeus fil., Suppl. Pl. 64, 1781. St. John, Taxon 12 (5): 201-204, 1963.

P. verus Rumph., Herb. Amb. 4: 139. t. 74. 1743; Kurz, J. Bot. Brit. & For. 5: 125, 1867, in part.

Keura odorifera Forsskal, Fl. Aegypt.-Arab. 172, 1775;

Pandanus odorifera (Forssk.) Kuntze, Rev. Gen. 2: 737, 1891. (Nomen dubium).

P. fascicularis Lamarck, Encycl. 1: 372, 1783.

P. leucanthus Hasskarl, Fl. Bot. Ztg. 25 (2), Beibl. 14, 1842.

Hasskarlia leucacantha Walpers, Ann. 1: 753.

Note: this is by no means all the older synonyms, but a full account of these is impossible until their exact identities have been set forth, since earlier authors, including Warburg, confounded the Indian-Malaysian species with the Polynesian-Melanesian species, and Warburg gave to this very broadly conceived species the name *Pandanus tectorius* Solander ex Parkinson, a name which is now agreed not to have been validly published (see Airy Shaw, Taxon 11 (7): 223, 1962) and therefore dates only from Warburg's publication in 1900. Neither his taxonomic nor his nomenclatural conclusions can be supported now; and the name *P. odoratissimus* L.f., though later than *Keura odorifera* Forsskal, will be the type of the genus *Pandanus*, since it has been shown by St. John to be better established. Forsskal's name must remain dubious, as it lacks a type specimen and was based only on part of a male flower. The species of the Pacific are distinctive enough to merit retention, though the number of binomials existing now is certainly too large; but even if a very widespread specific concept is adopted, it seems clear at this stage that *P. odoratissimus* is easily discriminated, both on vegetative and fruit characters, and its presently known range does not extend east of Malesia (in the sense of van Steenis in "Flora Malesiana"). The boundary is not certainly known but seems to be in the general vicinity of Wallace's Line. The Pacific species (or one of them) however appears to overlap the above area, and occurs at least in eastern Malesia; it is this occurrence which has helped to foster the confusion of the species. The plant illustrated in Rumphius' Tab. 81 seems to me to be an example of such overlapping. What name, or names, may be used for this plant and its Pacific relatives is a problem that can safely be deferred for the present.

NEW SYNONYMS: MALAYAN TYPE LOCALITIES:

- P. albibracteatus* St. John, *Pac. Sci.* 17: 10. 1963.
P. ambiglaucus St. John, *ibid.* 17: 13. 1963.
P. carnosus St. John, *ibid.* 17: 20. 1963.
P. globosus St. John, *ibid.* 17: 21. 1963.
P. inclinatus St. John, *ibid.* 17: 24. 1963.
P. incrassatus St. John, *ibid.* 17: 26. 1963.
P. obtusus St. John, *ibid.* 17: 28. 1963.
P. rubricoloratus St. John, *ibid.* 17: 32. 1963.
P. Boryi Gaud. *Voy. Bonite*, t. 22, f. 15. 1841; *em. St. John, ibid.* 17: 18. 1963.

ANAMBA ISLANDS:

- P. Hendersonii* St. John, *ibid.* 19: 116. 1965.

VIET NAM:

- P. integriapicis* St. John, *ibid.* 16: 91. 1962.
P. Phamhoangii St. John, *ibid.* 16: 96. 1962.
P. projectens St. John, *ibid.* 16: 100. 1962.
P. reversispiralis St. John, *ibid.* 16: 101. 1962.
P. semiorbicularis St. John, *ibid.* 16: 106. 1962.
P. Smitinandii St. John, *ibid.* 16: 109. 1962.
P. subcarnosus St. John, *ibid.* 16: 111. 1962.
P. subulatus St. John, *ibid.* 16: 114. 1962.
P. vietnamensis St. John, *ibid.* 16: 116. 1962.

HONG KONG:

- P. remotus* St. John, *ibid.* 16: 70. 1962.

MALDIVE ISLANDS:

- P. adduensis* St. John, *ibid.* 15: 328. 1961.
P. Hartmannii St. John, *ibid.* 15: 333. 1961.
P. Karikayo St. John, *ibid.* 15: 335. 1961.
P. maldivecus St. John, *ibid.* 15: 339. 1961.

DESCRIPTION:

(Figs. 1-6).

Habit. Coarsely branched trees with a tendency to candelabriform branching, the secondary branches sympodial by development of a lateral vegetative bud at the base of the terminal inflorescence; branching di- or trichotomous, or irregular. Main stem rarely more than 20 cm. thick, erect or more or less decumbent, usually thickest a little above the extreme base; later branches of the same or lesser diameter because of lack of cambium; leaves of three- to five-year-old vigorous juveniles often four or five times longer and twice or three times broader than leaves of senescent, much-branched adult plants. Main stem and not rarely upper stem and lower branches producing prop-roots up to 10 cm. thick, but usually more slender. Adult plant seldom over 10 m. tall; suckering from base occasional. Occurrence in groves not uncommon.

Stems green in growing stages towards apex, earliest parts white, soon discoloring on exposure, but covered by leaves; exposed part usually turned pale buff or gray-brown, grossly ringed by leaf-scars, these as much as 3-4 cm. apart on rapidly-grown parts, usually 1 cm. apart or a little less. Uppermost ultimate branches as slender as 3 cm. diameter in old trees. Base of branch at attachment to stem dorsoventrally flattened and somewhat clasping. Stems and branches usually more or less prickly because of blunt or acute adventitious roots with arrested growth, up to about 1 cm. long.

Leaves spiralled, in three rows (tristichies), clasping at base around the stem, the extreme edges just meeting there or slightly overlapping. Leaf margins of the clasping portion gradually thinner toward the edge, whitish or pale green. Blade ensiform, nearly parallel-sided, toward the apex very gradually reduced (in foliage leaves), more abruptly reduced in prophylls. Prophylls deltoid (approaching isosceles form), entire, the first one channelled on both sides, the remainder channelled ventrally, the series merging gradually to foliage-leaf form, with the last few prophylls (usually around the 9th) developing marginal prickles toward the apex; early foliage-leaves short, rather bluntly acute, marginal prickles developed; later ones with dorsal midrib prickles developed, and apices increasingly prolonged; adult foliage-leaves with the apex gradually narrowed into an elongated triquete flagella, the margins and dorsal midrib armed with prickles. Largest leaves as much as 3 m. long and 9 cm. broad, but usually less, 1-2 m. long and 4-7 cm. broad; length : width ratio commonly between 20:1 and 30:1. Blade M-shaped in section. Apex of youngest leaves stiffly erect, but older leaves drooping from near the tip or the midpoint or even lower. Dorsal surface glaucous on each side of the midrib; ventral surface also glaucous, but less so. Prickles *white*, or the extreme tip dark, commonly 3-5 mm. long, often longer; in some forms up to 10 mm. long, slender, very sharp, very slightly curved; prickles of margins all forwardly directed; prickles of midrib forwardly directed in the

distal half (approximately) of the leaf, but the prickles of the proximal part retrorse. Spacing of the prickles rather irregular, but distally the prickles always smaller and more crowded, proximally always larger and farther apart; commonly (near the leaf base) the prickles 1–3 cm. apart. (Some forms probably for genetic reasons unarmed). Parallel veins mostly 40–160, depending on age of leaf, age of tree, etc., visible but not prominent along most of the blade but less or not so toward the base. Transverse lines not at all evident, unless under microscope. Colored pigmentation absent, i.e. leaves never reddish, purplish, etc.; white- or yellow-striped variegated forms may exist.

Female inflorescence borne only on female trees, terminal, pedunculate, the peduncle 10–30 (rarely more) cm. long, trigonal, bracteate, the lower bracts leaflike, upper bracts whitish-yellow, successively shorter, more or less navicular, the midrib and margins with reduced prickles, texture sub-fleshy, the last bracts much reduced to linear-lanceolate shape and much shorter than the syncarp; these bracts all soon withering and more or less persistent but at last fragmenting and falling. Inflorescence a cephalium, globose to ellipsoid, up to about 30×20 cm., slightly rounded-trigonal, mostly $15\text{--}20$ cm. $\times$ $12\text{--}18$ cm.; composed of a variable number (26–143, usually about 50–70) of carpellate phalanges, these in turn composed of mostly 4–10 concentrically arranged fused carpels (phalanges of only 1–3 carpels or of 11–14 carpels rarely also occur, the former only near the cephalium apex, the latter only near the cephalium base). Carpels each terminating in a single U- or V-shaped stigma; carpel apex truncate, low-rounded, or low-pyramidal, sometimes somewhat acute. Phalanges laterally mostly smooth, rarely with 1 or 2 intercarpellary grooves; apically with slight grooves between the carpel tips. At maturity the phalanges red-orange to vermilion, sometimes the carpel tips still greenish; median part of phalange rather abruptly expanded into fleshy shoulders, these not evident in dried or insect-damaged or animal-gnawed specimens, but always obvious in fresh fully ripe fruit. Phalanges mostly 3–8 cm. long, 2.5–4.5 cm. wide, pentagonal or hexagonal but sometimes slightly exceeding these measurements; phalanges from cephalium base (peduncular end) always curved, shorter, and with more carpels, than those from lateral or apical part of cephalium; phalanges from apex of cephalium usually longest and with fewest carpels, the carpel tips more expanded and sometimes more acute. Young phalanges greenish-white, later yellow, finally orange then reddish to vermilion. Phalanges free of each other but tightly crowded; eventually falling from the cephalium receptacle, apical ones first, leaving a pentagonal or hexagonal scar. Cephalium when mature more or less drooping; when young usually suberect. Phalange externally covered by a pericarp; within this the upper mesocarp is lacunose, each carpel apex with a chamber traversed around the periphery by longitudinal fibers and crossed by thin plates of pithy tissues (aerenchyma); lower mesocarp fibrous, the fibers traversing a pulpy tissue;

endocarp central, osseous, reddish-brown, unitary, each carpel represented by one ovular chamber, this fusiform, a few fibers traversing the endocarp, some central in the mesocarp and leading to the stigma, these entering the ovular chamber along one side; upper part of ovular chamber filled with soft white endosperm; embryo basal; germinating downward. Outermost seeds often not developing.

Male inflorescence only on male trees, pedunculate, bracteate, the bracts similar in color and form to those of the female, but the inflorescence a raceme of spikes (an odd number, usually 5, 7, 9, or 11), each in the axil of a bract, each consisting of a fleshy central axis from which emerge numerous lateral phalanges of stamens about 13 mm. long, bearing about 19–23 stamens on short filaments 0.5–2 mm. long, with anthers 2–3.5 mm. long, narrowly sagittate, with an apiculum 0.5 mm. long; the basal part of the phalange is about 3 mm. long up to the first filament. The phalange, and the receptacle and major axis as well, are all clearly seen to be fasciculate. The overall length of the whole inflorescence varies from about 30 to 60 cm. long; the bracts subtending the spikes are mostly less than 30 cm. long, the last ones only about 6 cm. long. The inflorescence is ephemeral and decays very rapidly after maturing, usually within a couple of days.

Citation of specimens. No attempt is made here to cite all specimens of *Pandanus odoratissimus*, since it has been collected many, many times; and indeed many specimens are not worth the paper they are mounted on, for lack of representative parts, poor labelling, and so on. The specimens cited here are simply those of the herbaria at the Singapore Botanic Gardens and at the University of Malaya. The main purpose in citing these is to mark precisely those which are in fact this species to distinguish them from the very similar plants (often in villages) which have recently been called *P. spurius* Miq., and those which represent the Pacific-Melanesian group which has been called *P. tectorius*, such as *Lam* 3285.

MALAYA. Singapore: Changi, Dec. 1892, *Ridley* (♀). Bajau, 9 May 1892, *J. S. G.* (♂). Passu Panjan, 1901, *Ridley* (♂). Same locality, 1909, *Ridley* 14157 (♂). Kranji, mangrove swamps, 10 April 1966, *Stone* 6237, 6238 (♀), KLU. — Johore: Tanjong Bungah, 1894, *Ridley* 6284 (♂). Tana Panti, 22 April 1890, *Ridley* 4594 (♂). Kukul, May 1909, *Ridley* 14169 (♂). Tana Panti, 1892, *Ridley* (♀). Jason Bay, 15 June 1934, *Corner* (♂). 3 miles west of Kuala Sendai, 7 June 1922, *Goodall* (♂). Johore Bahru, west side mangrove area, 21 Nov. 1965, *Stone* 6106 (♀, KLU). Same locality, 12 April 1966, *Stone* 6106-A (♀, obs. ♂, KLU). Mersing, 6 Jan. 1959, *Paine* (♀). — Malacca: Near Malacca, 1892, *Ridley* (♂). "Sea-shore", 1 May 1895, *Maheiros* (sterile). — Negri Sembilan: Kuala Pilah, kampong pandan, 26 Feb. 1936, *Corner* SFN 30762 (♂). — Pahang: Kuala Pahang, 17 May 1890, *Ridley* (♂); 10 May 1890, *Ridley*

(♀). — Trengganu: Kuala Trengganu, 9 May 1925, *Holtum* SFN 15169 (♂). Cherating River, 25 Aug. 1884, *Ridley* (sterile). — Perak: Dindings, Pangkor, March 1896, *Ridley* (♂). Pulau Lalang, 30 Dec. 1925, *Sermund* (♂). Langkawi: April 1892, *Curtis* (♂). Penang: Batu Ferringhi, Tanjong Bungah, 10 Feb. 1966, *Stone* 6171, (♀); 2 May 1966, *Stone* 6350 (♀) KLU. [SING unless otherwise noted].

SUMATRA. Atjeh, Troemon, 27 Aug. 1941, *Asdat* 107. (♀).

PULAU BANGKEI: 30 June 1936, *Lütjeharms* 5134. (♀).

NORTH BORNEO: SABAH: Sibubu River, Mengalong Forest Reserve, 5 miles S. W. of Sipitang, 30 July 1954, *Wood & Wyatt-Smith* SAN 'A' 4567 (♀).

Some Forms of the species:

Pandanus odoratissimus L.f. forma *vietnamensis* (St. John) B. C. Stone, comb. et stat. nov.

P. vietnamensis St. John, Pac. Sci. 16: 116. f. 93. 1962.

Holotype: Vietnam, 6 km e. of Mui Ne, Phan Thiet Province, top of beach, 9 Feb. 1960, *St. John* 26,342 (BISH).

This seems to be distinctive in its unusually long prickles; those on the leaf base up to 11 mm. long; in the large cephalium, 27 cm. long, 19 cm. thick, with 106 phalanges; and in the stout phalanges of 5–9, usually 6–7 carpels, about 6 cm. long and 4 cm. thick.

Pandanus odoratissimus L.f. forma *karikayo* (St. John) B. C. Stone, comb. et stat. nov.

P. Karikayo St. John, Pac. Sci. 15: 335. f. 16. 1961.

P. adduensis St. John, *ibid.* 15: 328. f. 12. 1961.

P. Hartmannii St. John, *ibid.* 15: 333. f. 15. 1961.

Holotype: Maldive Islands: Fadiffolu Atoll, Kuredu Islet, Shore, 25 Sept. 1957, *W. D. Hartmann* 1 (A).

This form may be tenable because of the larger number of carpels per phalange, usually from 9 to 14.

Pandanus odoratissimus L.f. forma *rubricoloratus* (St. John) B. C. Stone, comb. et stat. nov.

P. rubricoloratus St. John, Pac. Sci. 17: 32, f. 163. 1963.

Holotype: Malaya: Pahang; Pulau Tioman, Telok Paya, sealevel, 19 May 1927, *M. R. Henderson* 18,444 (SING).

Rather distinctive because of its small globose cephalium only 9×8.5 cm., with 34 phalanges, each about 3.6×2.5 cm., the stigmas somewhat elevated.

Pandanus odoratissimus L.f. forma *hueensis* (St. John) B. C. Stone, comb. et stat. nov.

Pandanus hueensis St. John, Pac. Sci. 16: 88. f. 60. 1961.

Holotype: Vietnam: Thai Duong Ha, Hue, thicket at edge of brackish marsh by inner beach, sandy soil, 2 m. alt., 3 April, 1960, H. St. John 26,343 (BISH).

This seems to have certain characters permitting it to be ranked, at least for the time being, as a forma, although its relationship to *P. odoratissimus* is certainly very close. The important features are these: the short prickles, which even at the leaf base are only 2–4 mm. long (but white!); the large cephalium, 28×20 cm., with 143 phalanges; the large, rather narrow phalanges, about 7.4–8 cm. long and 2.8–4.6 cm. thick, with 4–9 carpels; and the high position of the endocarp, in the upper third of the phalange.

Summary and post-script.

Pandanus odoratissimus L.f. (Sect. *Pandanus*), the type species of the genus, was described from a male flowering specimen from Ceylon. A neotype collection has been made by Prof. H. St. John (Pac. Sci., in sched.) to establish the identity of the female plant, particularly the fruit: cf. Fig. 6. This is a coastal species, and the phalanges are distributed by ocean-currents. It is to be expected then that it should have a fairly wide distribution, in the manner of most coastal plants with oceanic dispersal, e.g. *Ipomoea pes-caprae*, *Canavalia rosea*, *Hernandia sonora*, *Heritiera littoralis*, etc. Nonetheless a very large number of species have been described, especially in the last few years, on the basis of specimens which are agreed to be close relatives (at least) of *P. odoratissimus*. By means of an analysis of the taxonomic criteria involved, and a tabular comparison of the alleged distinguishing features, it is belived to be evident that only one species can be distinguished, but it is clearly rather polymorphic, and hence several formae may be recognized. Although there are still no doubt further synonyms among the relevant binomials in existence, it is already possible to confirm that the broad concept of Warburg (1900) who considered that only one species ranged from the Indian Ocean to the limits of Polynesia, is erroneous; and that instead, there are undoubtedly a few distinct species in the Pacific Islands, though certainly fewer than the available binomials in existence would indicate. One of the Pacific species has borne the name *Pandanus tectorius*, which however is considered now to date validly only from its publication by Warburg in 1900, and not from Parkinson, 1773. Consequently another name must be found for the species (singular or plural) of Tahiti; several are available, including *Pandanus douglasii* Gaudich. (1841) which has already been used for the Hawaiian plants (manifestly of only one species) which certainly also occurs in Tahiti and no doubt elsewhere in Polynesia. How many species of this general 'Pacific' alliance can finally be discriminated, it is too early to tell; but it is certain that none penetrates into the Indian Ocean, at least not to the Maldives or beyond, and apparently throughout that area and in Malaysia (Malesia) the vicariant representative species is *P. odoratissimus*. Nonetheless, a member of this 'tectorius' group does overlap into the area of *P. odoratissimus*, evidently in the general region of

Wallacea, i.e. in parts of the Malayan-Indonesian Archipelago, particularly in the vicinity of Celebes-Amboina-Halmaheira, as also perhaps on the eastern coast of the Philippines.

Pandanus odoratissimus owes a number of its synonyms and in general much of the confusion surrounding the species is also due to the ephemeral nature of one of the major characteristics of the species, namely the abrupt fleshy dark red shoulders of the mature phalanges. Immature fruits, even when seen in the field, lack these; dried fruits, even when collected fully mature, also lack them (due to shrinkage); and many field-collected fruits lack them from depredations of ants or other insects. Consequently, this character, so effective in defining *P. odoratissimus*, has either been missed or ignored by most previous authorities. The other major character is the nature of the large, white spines of the leaves. By itself, this feature of armature must have seemed of secondary importance to earlier botanists; yet in conjunction with the fleshy shoulders, it is the hallmark of the species. *Neither character is found in the Pacific Islands beyond Malaysia.* Instead, these plants — whether of one, or as I rather believe, a few closely related species — have no shoulders on the phalanges, or if present, these are orange or vermilion, merely slightly bulging and never abrupt or dark red, and persisting after drying, i.e. not merely consisting of pulpy exocarp; and further, the leaves bear shorter, green spines, rarely as much as 4 mm. long, in contrast to those of *P. odoratissimus*, which may reach a length of 8 or 10 mm. Other distinguishing features will no doubt be found to correlate with these two obvious ones.

The western limit of *P. odoratissimus* appears to be the Maldive Islands of the Indian Ocean, although I suspect that *P. balfourii* Martelli of the Seychelle Islands is merely a form; but nothing like the species has ever been recorded from Mauritius, Madagascar, or the South African coast. Rendle's *P. rabaiensis* needs reviewing in the light of the above discussion also; this was from Mombasa — Dar-es-Salaam.

The eastern limit of *P. odoratissimus* seems to be along Wallace's Line, approximately. Field investigations in this region are critically needed. The status of *P. coronatus* Martelli (Philippines) must be reviewed. The distribution clearly extends northward into the Ryukyu Islands (cf. *P. tectorius* var. *liukiensis* Warb., and var. *ferreus* Y. Kimura). No doubt also Warburg's *P. tectorius* var. *sinensis* pertains to *P. odoratissimus*. *Exploration on these borders is a major desideratum*, for only until these borders are fully known can the questions relating to distribution be approached.

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TABLE I — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF PANDANUS

Species	Syncarp size + shape (all syncarps pendent at last); ped = peduncle	No. of carpels per phalange/ No. of phalanges per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. albibracteatatus</i> St. John	1, 23 × 17.5 cm. subglobose ped. 27 cm.	4 — 7 / 67 ph.	55 — 62 × 25 — 40 mm. <i>green—pink</i> orange-red	usu. none rarely 1 — 2	yes	yes / 35	Penang sea beach	1.7 — 2 m. 5 — 5.5 cm. spine tips reddish-brown
<i>P. ambiglaucus</i> St. John ..	1, 21 × 16 cm. ellipsoid ped. 40 cm.	7 — 8 / 85 ph.	60 — 66 × 28 — 40 mm.	none	no (but immature) !	no / 44 — 46	Singapore, Kranji, fresh water swamp	2 — 2.5 m. 5.8 — 6.3 cm. spines white
<i>P. Boryi</i> Gaud. ..	1, (16 × 14 cm.) Small cylindric (ellipsoid) red when ripe (ped. 22 cm.)	6 (— 10) / ?	63 × 28 — 34 mm. (55 — 60 × 20 — 34) <i>green—brown</i> yellowish	none	yes	no / 39 — 45	Singapore edge of "dry" mangrove swamp	1.7 m. × 3.5 cm. prickles "pale" or on midrib "reddish"

TABLE I — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF PANDANUS — continued

Species	Syncarp size + shape (all syncarps pendent at last); ped = peduncle	No. of carpels per phalange/ No. of phalanges per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. carnosus</i> St. John ..	1, 18 × 15 cm. subglobose	6 — 10 / ?	67 — 73 × 24 — 35 mm. partly green red-orange	none	yes	no / 45	Singapore, Kranji village Pahang-Kuantan	1.8 — 2.4 m. × 4.4 — 5.2 cm. spines pale but reddish-tipped
<i>P. globosus</i> St. John ..	1, 8.8 × 8.8 cm. globose ped. 9 cm.	5 — 6 / 26	36 — 39 × 22 — 28 mm.	none	no, but very immature	no / 38	Pulau Langkawi on limestone coast Celebes Borneo-Pulau Is.	81 — 90 cm. × 3.5 cm. prickles "Brown tipped"
<i>P. inclinatus</i> St. John ..	1, 16 — 23 cm. × 13 — 20 cm. subglobose ped. 30 cm.	(6) (7 — 9) (12) rarely doubled — 18 / 44 — 61	60 — 68 × 23 — 43 mm. greenish orange-red	none	yes	no / 38 — 40	Singapore, Kranji, brackish swamp	1.5 — 1.7 m. × 4.4 — 4.7 cm. spines all white with brown tips

TABLE I — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF *PANDANUS*—continued

Species	Syn carp size + shape (all syncarps pendant at last); ped = peduncle	No. of carpels per phalange/ No. of phalanges per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. incrassatus</i> St. John ..	1, 15 × 14.5 cm. ped. 23 cm.	5—8 /54	46—52 × 23—36 mm. <i>green</i> red-orange	none	yes	no /34 — 35	Singapore, Kranji	1.4 — 1.7 × 4.2 cm. spines white, brown-tipped
<i>P. obtusus</i> St. John ..	1, c. 12 × 12 cm. ped. 23+ cm.	8—10 /38	50—55 × 27—38 mm. (dried) <u>brown</u>	none	no, but <i>immature</i>	no /21 — 39	Pahang- <i>Kuantan</i> Singapore	0.8 — 1.3 m. × 3.4 cm. prickles pale but reddish
<i>P. rubricoloratus</i> St. John	1, 9 × 8.5 cm. ped. 15+ cm.	6—9 /34	36 × 20 — 27 mm. <i>red</i> <i>red</i>	none	yes	no /27	Pulau Tioman	66 — 73 × 2.8 — 3 cm. prickles pale + brown- tipped

TABLE I — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF PANDANUS—continued

Species	Syncarp size + shape (all syncarps pendent at last); ped = peduncle	No. of carpels per phalange/ No. of phalanges per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. remotus</i> St. John ..	1, 23 × 18 — 20 cm. ellipsoid ped. 20 cm.	(7) (8—9) 10 /50+	42 × 46 — 16 — 30 mm. yellow orange	a few or other partial ones but shallow	yes	yes / ?	Hongkong	0.95—1.6 m. × 4.5 cm. prickles yellowish
<i>P. hueensis</i> St. John ..	1, 28 × 20 cm. elliptic-ovoid ped. 30 cm.	(5—) 6—7 (—9) /143	74 — 80 × 28 — 46 mm. orange yellow	none	no (apparently)	no / ?	Vietnam	1.4—1.6 m. × 4.7 — 5.5 cm. <i>small</i> spines white often browntipped
<i>P. integrilapicis</i> St. John	1, 17 × 10 — 11 cm.	7 — 9 /74	27 — 31 × 18 — 30 mm. green orange	none	yes	no / ?	Vietnam	78 — 87 × 4.2 — 4.5 cm. large pale prickles; tip almost devoid of prickles!

TABLE I — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF PANDANUS—continued

Species	Syncarp size + shape (all syncarps pendent at last); ped peduncle	No. of carpels per phalange/ No. of phalange/ per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. Phamhoangii</i> St. John	1 ₁ , 11—12.5 × 9—10.5 cm. ped. 15 cm.	5—8 /34	34—38 × 22—40 mm. green	none	no, but immature	no /?	Vietnam St. J. also reports spms. from Riouw Isls.	0.6—1.3 m. × 3.4—3.6 cm. prickles white often brown-tipped
<i>P. projectens</i> St. John	1 ₁ , 18.5 × 14.5 cm. ped. 10 + cm.	6—9 /82	42—46 × 22—40 mm. ? yellow	none	no, but immature	no /?	Vietnam	1.26 m. × 5 cm. prickles yellowish but brown-tipped
<i>P. reversispiralis</i> St. John	1 ₁ , 12—16 × 11—14 cm. ped. 20—25 cm.	5—7 /52—94	43—46 × 23—38 mm. orange	none or few very shallow ones	yes	yes /?	Vietnam	0.7—1.3 m. × 4.8—6 cm. prickles white, brown-tipped

TABLE I — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF PANDANUS—continued

Species	Syncarp size + shape (all syncarps pendent at last); ped = peduncle	No. of carpels per phalange/ No. of phalanges per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. semiobacularis</i> St. John	1, 17 × 14.5 cm. ped.	(5) (7—8) (10) /86	45—50 × 24—43 mm. green— orange	same as above	no, but immature	yes /?	Vietnam	0.8—1 cm. × 4.5—5 cm.
<i>P. Smitinandii</i> St. John ..	1, 14 × 11.5 cm.	6—12 (8—9) /72	40—43 × 21—33 mm. green yellowish	none or few	no, but immature	no /?	Vietnam dunes	1—1.15 m. × 4.3—4.8 cm. prickles “straw- color”
<i>P. subcarnosus</i> St. John ..	1, 16 × 14 cm. orange ped. 20 cm.	6—10 (7—8) /84	45—49 × 22—42 mm. orange	none	yes	no /?	Vietnam	1—1.13 m. × 3.7—4 cm. prickles white
<i>P. subulatus</i> St. John ..	1, 10—12 × 10 cm. ped. 15—20 cm.	5 (—6) /47—73	35—41 × 18—33 mm. orange	none	no, but slightly immature	no /?	Vietnam	70—74 × 4 cm. prickles white

TABLE I — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF *PANDANUS*—continued

Species	Syncarp size + shape (all syncarps pendent at last; ped = peduncle)	No. of carpels per phalange/ No. of phalanges per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. vietnamensis</i> St. John	27 × 19 cm. scarlet—red ped. 30 cm.	5—9 (6—7) /106	58—60 × 25—42 mm. scarlet + orange-red yellowish	none	yes	no /?	Vietnam	1—1.5 m. × 5—6 cm. prickles white lower spines to 11 mm.
<i>P. Hendersonii</i> St. John ..	1, 19 × 11 cm. ped. 20+ cm.	7—11 (8—10) /70	(39—45) — 50) × 24—40 mm.	none	yes	no /38—42	Indonesia Anamba Isl.	1—1.5 m. × 4—5 cm. prickles pale, brown-tipped
<i>P. adduensis</i> St. John ..	?	9—13	4.5—4.9 × 3.4—4.1 cm.	none	?	no	Maldiv Islands	1.5 m. × 6.3 cm. prickles brown-tipped

TABLE 1 — COMPARISON OF THE DIAGNOSTIC FEATURES OF 25 PROPOSED SPECIES OF PANDANUS—continued

Species	Syncarp size + shape (all syncarps pendent at last); ped = peduncle	No. of carpels per phalange/ No. of phalanges per cephalium	Size + Shape of phalanges + color	Lateral sutures present or not	With fleshy shoulders or not	Male known / # of veins per lf. half	Locality, ecol.	Leaves: length × width; Spine details
<i>P. Hartmannii</i> St. John ..	20 × 14 cm. ellipsoid	12 (— 14)	4 — 4.3 × 2.8 — 4 cm.	none (or very few shallow)	?	no	Maldiv Islands	1.2 m. × 5.7 cm. "dark tips" on prickles
<i>P. Karikayo</i> St. John ..	18 × 13 cm. "Bright red"	10 — 14	3.8 — 4.4 × 2 — 3.4 cm.	none	?	no	Maldiv Islands	1 — 1.25 (— 3?) m. × 5.2 cm. "pale"
<i>P. Maldivicus</i> ..	14 × 11 cm. broad ellipsoid	5 — 9, usu. 6 /60	4.8 — 5.2 × 2.2 — 3.4 cm.	none	?	no	Maldiv Islands	1.17 m. × 4 — 5 cm. "dark- tipped" prickles



Figure 1

Pandanus odoratissimus L.f. A fruiting female tree about 8 m. tall, on the sandy beach at Tanjong Bungah, north coast of Penang (Stone 6171), near the type locality of *P. albibracteatus*.



Figure 2

Pandanus odoratissimus L.f. A young plant in the Singapore Botanic Gardens.

Above, view of the whole plant. Note the numerous small leafy branches near the base at left.

Below, midportions of several leaves showing the ventral surfaces. Note the slender, elongated, white marginal prickles.

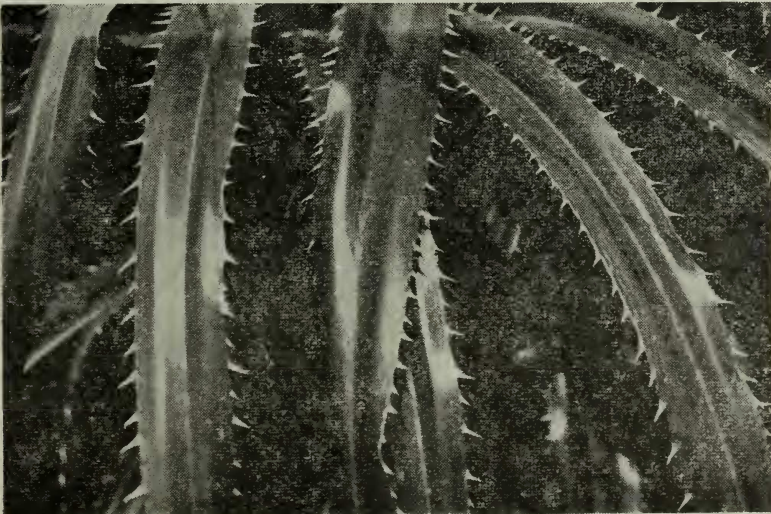




Figure 3

Mature cephalium of *Pandanus odoratissimus* L.f. (Stone 6171 from Penang). The color is red-orange or vermillion; a few carpel tips are still green.



Figure 4

Cephalia of *Pandanus odoratissimus* L.f. (Stone 6171 from Penang).

Above, an unripe young cephalium.

Below, a ripe cephalium cut in half.



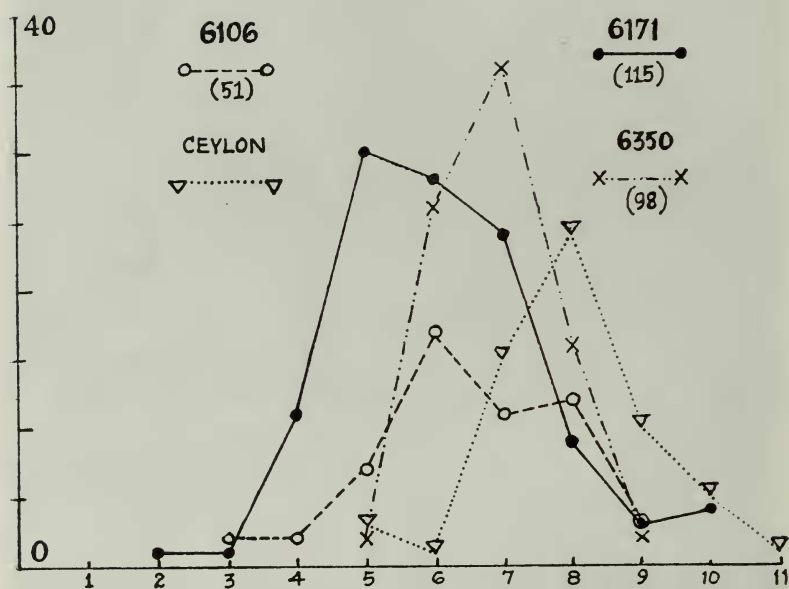


Figure 5

Carpel numbers in *Pandanus odoratissimus* L.f.

The vertical axis shows number of phalanges; the horizontal axis shows number of carpels per phalange. Whole-cephalium samples only are used. The numbers above the sample line refer to collections. The number in parentheses below the sample line indicate the total number of phalanges borne by the cephalium. No. 6106 is from Johore; no. 6171 is from Penang; and no. 6350 is from Penang. Major carpal numbers are: for 6106 6; for 6171, 5; and for 6350, 7. The total range is 2–10. Individual ranges are: for 6106, 3–9; for 6171, 2–10; for 6350, 5–9. It should be added that two additional cephalia, not shown graphically here, from the same individual as 6106, gave the following data: (a) total phalanges 40; range 5–9; major carpal number 7. (b) total phalanges 47; range 4–8; major carpal number 7. The Ceylon sample (*St. John* 24212) shows a major carpal number 8; the range is 5–11; total phalanges 59.

Note.—Strictly, these graphs should be histograms, but in order to conserve space, lines have been used so that several samples may be superimposed. The variation between each carpal number is of course not continuous.

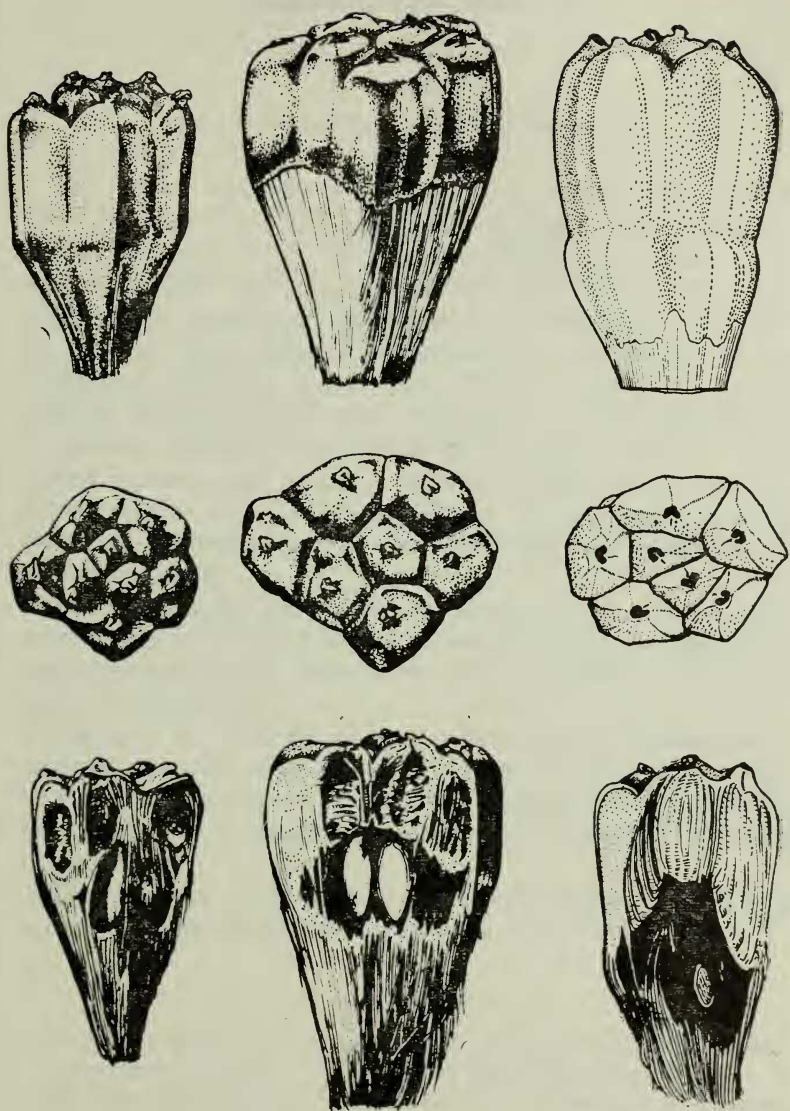


Figure 6

Phalanges of *Pandanus odoratissimus* L.f.

Left: profile, top view, and sectional view of *St. John* 24212 from Ceylon.

Centre: profile, top view, and sectional view of *St. John* 24218 from Ceylon.

Right: profile, top view, and sectional view of *Stone* 6350 from Penang (Natural size).